

Energy budget contextualization of fish biomasses at B_{MSY}

GARM3 System Capacity Analyses
Biological Reference Point Meeting

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Introduction:

This Working paper addresses TOR 3 of the GARM BRP Meeting: Ecosystem Approaches to Gulf of Maine/Georges Bank fisheries. It provides analyses to determine if the Northeast Shelf LME (Large Marine Ecosystem) can support the reference point biomasses (summed BRPs) required for the GARM species (see NEFSC 2002) as well as the other demersal and pelagic fish resources in the region. There has been some concern expressed by various stakeholders as to whether the US Northeast Shelf LME can support biomass at optimal levels (e.g., B_{MSY}) simultaneously for all 19 groundfish (GARM species), and more broadly, the entire fish community.

The purpose of this working paper is to contextualize the finfish species in a broader ecosystem context. Specifically, the estimates of commercially important fish at various levels of biomass, as well as other, non-targeted fish species, were examined in a previously established balanced energy budget (Link et al. 2006). The aim was to take the balanced energy budget and then perturb it under different scenarios to see if then upon rebalancing, how the ecological network would redistribute biomass and if the biomass scenarios would be feasible given ecological systemic constraints. This work explicitly builds upon WP 3.1 (and estimates of MSY; c.f. NEFSC 2002, 2003, 2007) which summarizes current information on the BRPs for GARM species and other fish components of the US Northeast Shelf LME.

Methods

The detailed methods of how we constructed and balanced the Gulf of Maine energy budget are provided elsewhere (Link et al. 2006). Very briefly, there are five

main elements critical to the construction of each node for this ecological network. We estimated biomass, production, consumption, respiration, and diet composition for all nodes. We provide examples of key rate processes in Table 1. Various approaches were used for all the nodes, ranging from literature bounding of values for some of the globally under-determined groups (e.g. bacteria, microzooplankton) to probabilistic estimates from multiple sampling regimes (e.g. some of the fishes). For further details of how we parameterized, initialized and balanced the network, see Link et al. (2006; part of our Energy Modeling and Analysis eXercise (EMAX)).

The EMAX effort utilized 36 biomass nodes in the network, which were parameterized for the four regions in the Northeast U.S. Large Marine Ecosystem. Table 2 shows the biomass estimates for all the regions. We combined these estimates into one model for entire NEUS LME. After combining the biomasses (weighted average by the area of each region), we then rebalanced the model to obtain a baseline from which we could compare the various scenarios (Table 3). Additionally, for some nodes it was germane to estimate other sources of removals- namely fisheries removals, bycatch, or ship-strikes- which are presented in Table 4. The present effort utilizes solely the Ecopath ecological network software package (Christensen and Pauly 1992, Walters et al. 1997) although the EMAX effort used additional software programs.

The basic energy balance model equation for each node in Ecopath can be expressed as:

$$C_i = P_i + R_i + E_i$$

where C_i is consumption, P_i is production R_i is respiration, and E_i is egestion (unassimilated food) of the i th node.

In Ecopath, the production for a closed system is given by:

$$P_i = Y_i + B_i(M2_i + MO_i)$$

where Y_i represents fishery removals (yield), B_i is biomass, $M2_i$ is predation mortality and MO_i is all other sources of mortality in the i th node. The model can be readily extended to include net import or export terms from each node and accumulation of biomass at each node. Other mortality (MO_i) can be expressed as:

$$MO_i = (1 - EE_i)P_i$$

where EE_i is the ecotrophic efficiency (fraction of total production that is utilized in the system; $0 < EE_i < 1$).

The mass balance model can then be expressed:

$$B_i(P/B)_i EE_i - Y_i - \sum_j B_j(C/B)_j DC_{ij} = 0$$

where again B_i is the biomass in node i , $(P/B)_i$ is the production to biomass ratio, EE_i is the ecotrophic efficiency; Y_i is the catch for node i ; B_j is the biomass and $(C/B)_j$ is the consumption to biomass ratio for predator j ; and DC_{ij} is the diet composition of predator j (fraction of biomass comprising prey i in the diet of predator). In the following, we have assumed no net migration during the time period considered.

Once we obtained the balanced baseline network, we then perturbed it under one of several scenarios (Table 5) and rebalanced the model with differing biomass inputs (Table 6). We did not execute a double demersal biomass scenario as effectively that was indistinguishable from the B_{MSY} scenario. There are four demersal (including medium pelagics) nodes and four small pelagic nodes. Some of these nodes contain solely targeted species (e.g., small pelagics commercial) whereas others are a mix of targeted and non-targeted species. For the various pelagic or demersal scenarios, we halved or

double all four nodes. For the B_{MSY} scenario we altered only those species that are targeted and did not alter the biomass of other, non-targeted species. Again, after the baseline model was perturbed in one of these scenarios, we executed a network rebalancing effort.

Ecopath employs a statistical balancing procedure to constrain the estimates for the underdetermined system of equations. We employed both minimizing the sum of excess Ecotrophic Efficiency (EE) and minimizing the maximum current EE in the Ecopath autobalance feature. Additionally, we used the Ecopath pedigree table to set confidence values for biomass, production:biomass (P:B), C:B, diet and catch for autobalancing. In EcoPath, we then rebalanced the baseline input using ecotrophic efficiency (EE) as the primary constraint, attempting to get as many nodes as possible to <0.9 . Again, further details about the general protocols can be found in Link et al. (2006).

We present our results as absolute and percentage difference of the rebalanced scenarios relative to the baseline. We also provide an accounting of the flows to detritus, given the noted caveats of how Ecopath utilizes this node in its balancing (Heymans and Baird 2000, Allesina and Bondavalli 2003, Link et al. 2006). Finally, we provide some of the systemic metrics that are routine outputs of this network model, along with some relatively simple summary indices, to compare and contrast major, systemic indices for each scenario.

Results and Discussion

The B_{MSY} scenario (Fig. 1a) shows that on an absolute basis small pelagics-commercial are predicted to notably increase in the rebalancing relative to the B_{MSY} inputs. Conversely demersal- benthivores and –piscivores notably decrease relative to the inputs. In effect, the model predicts that almost 1.3 million metric tons is moved from the demersals to the pelagics to rebalance the network. Relative to the baseline, there is minimal change in the final, balanced version of the modeled scenario. In terms of percent change (Fig. 1b), three of the four demersal nodes declined by a factor between ~90 and 200%. Here the small pelagic nodes categorically increased (by a factor of ~10 to 100%). These results can, upon first inspection, be interpreted that the forage base of the demersals needs to be increased to support the consumptive demands of the demersals, or else those demands need to be lowered, or a combination thereof, for the network to be rebalanced.

The doubling of small pelagics scenario (Fig 2) shows an absolute and percentage predicted increase in small pelagics-commercial, minimal changes in squids and other, and a slight increase in anadromous nodes relative to inputs. These absolute changes are lesser than the B_{MSY} scenario. Relative to the baseline, all the small pelagic nodes exhibit some form of increase except anadromous species, which shows a small decline. Most of the demersal nodes show an opposite, compensating change in biomass relative to inputs for this scenario, except demersal-omnivores which shows a slight increase. Conversely, relative to the baseline the demersal- benthivores show a predicted increase in biomass. Although less straightforward than the prior scenario, these results are interpreted similarly as in the B_{MSY} scenario.

The halving of small pelagics scenario (Fig 3) basically gets reset towards the baseline, with a final balanced version having all the small pelagic nodes increasing relative to the scenario inputs, albeit at lower values than the baseline. Similar to the B_{MSY} scenario, the demersal- benthivores and -piscivores are predicted to decline in the final, balanced version of this scenario.

The halving demersals scenario (Fig 4) shows a predicted increase in absolute and percentage demersal – omnivore biomass. Yet the largest and most surprising change is the large absolute increase in small pelagics- commercial and the three out of four small pelagic nodes exhibiting a large percentage increase in biomass. The increase in demersal omnivores is potentially explainable by the need to increase that node; whereas the other demersals did not change or were relatively less than both the input and baseline. Yet the predicted small pelagics response is potentially counter-intuitive and largely reflects a flow of biomass to the small pelagics (lower predation, lower competition, etc.).

The cybernetic metrics (Table 7) shows a wide range of indicators for a network, none of which exhibit notable differences across these scenarios as compared to the baseline. The doubling of pelagics scenario does show the most change in some of these metrics (e.g., exports, throughput, net production, PP/tot B, etc.) but these are relatively minor changes by most network metric standards.

The flows to detritus (Fig 5) show that when you halve biomass of major nodes, there is not that much change in detrital output. In the one scenario where biomass is increased (small pelagics), the flows to detritus increase by a factor of approximately 33 to 150%. The B_{MSY} scenario is similar in output to the baseline and halving biomass

scenarios. The implication of this is that when biomass is increased beyond what is within the range of the baseline, there is excess material shunted to outside of the system as a mechanism to achieve network balance. When the scenarios are within the range of the baseline, this change in detrital exports is not as strongly needed. Translated, as this model balances the changes, it either uses extant flows in the system to maintain the trophic balance (in an energetic budgetary sense) or shunts to/from detritus to maintain this balance. By increasing the flow to detritus, what the model is effectively doing is tuning to an unknown. What we can say that is if this as an indicator of detrital use is minimally changed, then there may be sufficient biomass production within the foodweb to support the changed biomasses without having to invoke detrital dynamics to achieve a balanced network.

The summary biomasses (Table 8) shows that the except for doubling small pelagics, all the outcomes in aggregate are quite similar. Even the doubling small pelagics is within the range of other reported ecosystems (WP 3.1). What this does show is the importance of allocation of biomass among specific fish nodes, allowing for some systemic-level compensation among interacting nodes.

There are four main summary observations. First, this ecosystem is productive and by most metrics there does not appear to be any major bottom-up limitations to the current or potential slight increases in fish biomass. Second, these results are just equilibrium rebalancing and do not account for responses in F. Third, it appears that some, but not necessarily all, of the fish components of the system could be increased relative to current biomass levels. Finally, it appears that overall, the final rebalanced

versions of the different scenarios had minimal change relative to balanced baseline network.

All of these predicted responses were from changes in biomass scenarios. Future efforts could look at changes in landings without changes in biomasses as a complimentary set of scenarios. How prominent those perturbations would be would need to be examined in this network context to account for all sources of removals (e.g. predation) simultaneously.

Now for a major caveat.

From this and previous work (NEFSC, unpubl. ms), the predicted Ecopath model results (from perturbations to a balanced energy budget) fall into one of three categories. First, some predicted model results were intuitive and in obvious agreement with established ecological and fishing theory. For instance, when one increases small pelagics and the final, balanced model has a predicted increase in small pelagics. Second, some predicted model results were counter-intuitive upon initial observation, seemingly contradictory to known ecological and fishing theory. But upon further examination the results were explainable given the constraints of an equilibrium energy budget. For example, when one decreases small pelagics and the final, balanced model has a concomitant decrease in demersals to balance the consumptive demand on the pelagics as forage. Finally, some predicted results were counter-intuitive and difficult to reconcile with theory or further examination of equilibrium constraints. For instance, interpreting our results for the halving demersals scenario and why small pelagics increased by such a factor. The challenge when using this software package in this type of exercise is to know with certainty in which of the three categories the results reside.

Conclusions

It is unclear if B_{MSY} for all species will be energy limited from a systemic perspective (c.f. cybernetic metrics, detrital flows, etc.), but certainly dynamics within a network node (in terms of total biomass) would need to be considered. Further, rebalancing relative to input values for these scenarios is unclear if the system would be able to simultaneously have all fish species at B_{MSY} due to flow constraints. Whenever we set demersals at high levels (~doubling them for the B_{MSY} scenario), the model effectively returned to the baseline situation.

All of the scenarios were balanced largely predicated upon a higher small pelagic-commercial biomass and a lower demersal- omnivore and piscivore biomass. How realistic these predictions are remains to be validated.

This approach provides broader context and places the groundfish species in a systemic context. However, given the uncertainties in model flow structuring sufficient to obtain a rebalanced network, coupled with a consistent increase in small pelagic biomasses regardless of initial scenario (potential “hardwiring” via the diet matrix in network parlance), we conclude that *this method and the results from it, although interesting, remain inconclusive* to answer the primary question. That is, although we may have achieved balance of the network, some structural caveats and misunderstandings of this modeling package likely remain on our part. Whether current harvest removal targets (MSYs) are attainable is also the subject of other studies for the GARM3, within which these results should be considered.

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Table 1. Major vital rates used for the NE US LME ecological network. P/B = production to biomass ratio, C/B = consumption to biomass ratio, Unassim. = amount of consumption that is unassimilated, loosely but not singularly related to respiration.

Group name	P/B	C/B	Unassim.
Phytoplankton- Primary Producers	180.666	0	0
Bacteria	91.25	380.208	0.2
Microzooplankton	72	242.424	0.1
Small copepods	45.22516	127.75	0.25
Large Copepods	55.34359	109.5	0.25
Gelatinous Zooplankton	38.39602	145.4831	0.35
Micronekton	14.25	89.5145	0.25
Mesopelagics	0.95	1.825	0.15
Macrobenthos- polychaetes	2.51604	17.5	0.5
Macrobenthos- crustaceans	3.096239	21	0.5
Macrobenthos- molluscs	2.076991	13.91018	0.6
Macrobenthos- other	2.02322	15.84646	0.5
Megabenthos- filterers	3.67319	15.93581	0.7
Megabenthos- other	1.896618	15.48902	0.3
Shrimp et al.	2	5	0.3
Larval-juv fish- all	18.01306	45	0.15
Small Pelagics- commercial	0.411876	1.962146	0.15
Small Pelagics- other	0.781218	2	0.35
Small Pelagics- squid	1.094358	2.509403	0.15
Small Pelagics- anadromous	0.43768	2	0.15
Medium Pelagics- (piscivores & other)	0.550492	1.745098	0.15
Demersals- benthivores	0.452887	0.903541	0.3
Demersals- omnivores	0.478872	0.83739	0.35
Demersals- piscivores	0.493127	1.263447	0.15
Sharks- coastal	0.101034	1.157974	0.15
Sharks- pelagics	0.117692	0.720229	0.15
HMS	0.553969	5.015501	0.15
Pinnipeds	0.084448	6.60733	0.2
Baleen Whales	0.040062	3.70679	0.2

Odontocetes	0.04026	13.4464	0.2
Sea Birds	0.275	9.285042	0.15
Discard	0	0	0
Detritus-POC	0	0	0

Table 2. Biomasses for all the nodes in each of the regions of the NE US LME. GB = Georges Bank, GOM = Gulf of Maine, MAB = Mid Atlantic Bight, SNE = Southern New England.

area km ²	GB 43666.16		GOM 79127.95		MAB 59807.29		SNE 64060.37	
Group name	Biomass in hab. area (t/km ²)	wted B	Biomass in hab. area (t/km ²)	wted B	Biomass in hab. area (t/km ²)	wted B	Biomass in hab. area (t/km ²)	wted B
Phytoplankton- Primary Producers	25.705	1122439	22.126	1750785	20.045	1198837	26.528	1699393
Bacteria	6.518	284616	5.484	433937.7	7.158	428100.6	7.532	482502.7
Microzooplankton	5.588	244006.5	4.885	386540.1	4.721	282350.2	5.083	325618.9
Small copepods	12.985	567005	10.403	823168.1	5.55	331930.5	11.825	757513.9
Large Copepods	6.981	304833.4	11.955	945974.7	4.512	269850.5	5.653	362133.3
Gelatinous Zooplankton	1.319	57595.66	1.283	101521.2	0.234	13994.91	1.196	76616.2
Micronekton	3.805	166149.7	4.874	385669.6	3.496	209086.3	4.233	271167.5
Mesopelagics	0.045	1964.977	0	0	0.181	10825.12	0.228	14605.76
Macrobenthos- polychaetes	11.403	497925.2	18.942	1498842	20.954	1253202	35.436	2270043
Macrobenthos- crustaceans	10.874	474825.8	4.04	319676.9	5.558	332408.9	6.392	409473.9
Macrobenthos- molluscs	9.887	431727.3	9.866	780676.4	32.885	1966763	17.805	1140595
Macrobenthos- other	40.023	1747651	24.936	1973135	32.447	1940567	18.933	1212855
Megabenthos- filterers	3.614	157809.5	2.879	227809.4	4.426	264707.1	3.702	237151.5
Megabenthos- other	3.965	173136.3	3.505	277343.5	3.508	209804	3.373	216075.6
Shrimp et al.	0.09	3929.954	0.396	31334.67	0.178	10645.7	0.27	17296.3
Larval-juv fish- all	0.629	27466.01	0.207	16379.49	0.166	9928.01	0.422	27033.48
Small Pelagics- commercial	14.977	653988	5.714	452137.1	5.738	343174.2	14.851	951360.6
Small Pelagics- other	1.074	46897.45	1.24	98118.66	2.494	149159.4	1.946	124661.5
Small Pelagics- squid	1.262	55106.69	0.275	21760.19	1.18	70572.6	3.07	196665.3
Small Pelagics- anadromous	0.25	10916.54	0.153	12106.58	0.507	30322.3	0.659	42215.78
Medium Pelagics- (piscivores & other)	0.292	12750.52	0.0229	1812.03	0.249	14892.02	0.35	22421.13
Demersals- benthivores	4.576	199816.3	2.981	235880.4	3.51	209923.6	2.337	149709.1
Demersals- omnivores	3.439	150167.9	0.4	31651.18	2.306	137915.6	3.635	232859.4
Demersals- piscivores	2.245	98030.52	4.006	316986.6	1.984	118657.7	2.334	149516.9

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Sharks- coastal	0	0	0	0	0.04	2392.292	0.0215	1377.298
Sharks- pelagics	0.0433	1890.745	0.00296	234.2187	0.0269	1608.816	0.0388	2485.542
HMS	0.0044	192.1311	0.00587	464.4811	0.032	1913.833	0.00548	351.0508
Pinnipeds	0	0	0.063	4985.061	0	0	0.0178	1140.275
Baleen Whales	0.417	18208.79	0.602	47635.03	0.16	9569.166	0.14	8968.452
Odontocetes	0.113	4934.276	0.0336	2658.699	0.0617	3690.11	0.0752	4817.34
Sea Birds	0.0035	152.8315	0.0035	276.9478	0.00295	176.4315	0.0107	685.446
Discard	0.484	21134.42	0.442	34974.56	1.269	75895.45	0.974	62394.8
Detritus-POC	50	2183308	81.333	6435714	30	1794219	40	2562415

Table 3. Combined biomasses (weighted averages) for all the nodes in the NE US LME ecological network.

Total	246661.8	Area in km2
	t km-2	mt
Group name	wtB avg for region	
Phytoplankton- Primary Producers	23.39825	
Bacteria	6.604822	
Microzooplankton	5.021109	
Small copepods	10.0527	
Large Copepods	7.633092	
Gelatinous Zooplankton	1.012431	
Micronekton	4.184164	
Mesopelagics	0.111067	
Macrobenthos- polychaetes	22.37887	
Macrobenthos- crustaceans	6.228714	
Macrobenthos- molluscs	17.51289	
Macrobenthos- other	27.86896	
Megabenthos- filterers	3.597953	
Megabenthos- other	3.552879	Base
Shrimp et al.	0.256248	
Larval-juv fish- all	0.327602	
Small Pelagics- commercial	9.732598	2400660
Small Pelagics- other	1.698021	418837
Small Pelagics- squid	1.395047	344104.8
Small Pelagics- anadromous	0.387418	95561.2
Medium Pelagics- (piscivores & other)	0.210311	51875.69
Demersals- benthivores	3.224373	795329.4
Demersals- omnivores	2.240291	552594.1
Demersals- piscivores	2.769751	683191.7
Sharks- coastal	0.015282	
Sharks- pelagics	0.025214	
HMS	0.011844	
Pinnipeds	0.024833	

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Baleen Whales	0.342094
Odontocetes	0.065273
Sea Birds	0.005237
Discard	0.788121
Detritus-POC	52.60505

Table 4. Combined landings (catch; includes shipstrikes for marine mammals) and discards (bycatch) for the nodes in the NE US LME ecological network.

Catch	t km-2		mt	Discards	t km-2		mt
Phytoplankton- Primary Producers		0	0	Phytoplankton- Primary Producers		0	0
Bacteria		0	0	Bacteria		0	0
Microzooplankton		0	0	Microzooplankton		0	0
Small copepods		0	0	Small copepods		0	0
Large Copepods		0	0	Large Copepods		0	0
Gelatinous Zooplankton	6.36E-07		0.156877	Gelatinous Zooplankton	2.11E-06		0.521196
Micronekton		0	0	Micronekton	0.019		4686.574
Mesopelagics	3.7E-12		9.13E-07	Mesopelagics	3.61E-10		8.9E-05
Macrobenthos- polychaetes		0	0	Macrobenthos- polychaetes	0.000613		151.2037
Macrobenthos- crustaceans		0	0	Macrobenthos- crustaceans	0.000113		27.77412
Macrobenthos- molluscs		0	0	Macrobenthos- molluscs	0.001277		314.9871
Macrobenthos- other	1.668		411431.8	Macrobenthos- other	0.650059		160344.7
Megabenthos- filterers	3.4167		842769.3	Megabenthos- filterers	1.4893		367353.4
Megabenthos- other	0.3594		88650.24	Megabenthos- other	0.16516		40738.66
Shrimp et al.	0.123		30339.4	Shrimp et al.	0.038729		9552.964
Larval-juv fish- all	0.44		108531.2	Larval-juv fish- all	0.299		73751.87
Small Pelagics- commercial	1.1144		274879.9	Small Pelagics- commercial	0.3448		85048.98
Small Pelagics- other	0.922955		227657.7	Small Pelagics- other	0.124646		30745.4
Small Pelagics- squid	0.285139		70332.89	Small Pelagics- squid	0.036382		8974.049
Small Pelagics- anadromous	0.24349		60059.67	Small Pelagics- anadromous	0.0891		21977.56
Medium Pelagics- (piscivores & other)	0.15575		38417.57	Medium Pelagics- (piscivores & other)	0.14093		34762.04
Demersals- benthivores	0.2681		66130.02	Demersals- benthivores	0.08601		21215.38
Demersals- omnivores	0.32787		80872.99	Demersals- omnivores	0.56168		138545
Demersals- piscivores	0.8281		204260.6	Demersals- piscivores	0.2848		70249.27
Sharks- coastal	0.0016		394.6588	Sharks- coastal	0.0025		616.6544
Sharks- pelagics	0.004518		1114.418	Sharks- pelagics	0.003895		960.7723
HMS	0.01304		3216.469	HMS	0.005875		1449.138
Pinnipeds		0	0	Pinnipeds	0.00115		283.661
Baleen Whales	1.25E-08		0.003083	Baleen Whales	0.000405		99.90441

Odontocetes	1.02E-08	0.002516	Odontocetes	0.000139	34.29237
Sea Birds	0.000144	35.51929	Sea Birds	0.000158	39.07122
Discard	0	0	Discard	0	0
Detritus-POC	0	0	Detritus-POC	0	0

Table 5. List of the main scenarios executed in this rebalancing analysis.

B_{MSY} for 8 fish groups
All small pelagics Biomass doubled from B_{MSY} values
All small pelagics Biomass halved from B_{MSY} values
All demersals Biomass halved from B_{MSY} values

Table 6. Initial biomass input values for the main fish nodes to be rebalanced and contrasted to the baseline scenario.

	Baseline-balanced		GARM Bmsy		Double Pelagics		Halve Pelagics		Halve Demersals	
	t km-2	mt	t km-3	mt	t km2	mt	t km2	mt	t km2	mt
Small Pelagics- commercial	10.509	2592169	5.2541	1295986	10.5082	2591971	2.62705	647992.8	5.2541	1295986
Small Pelagics- other	2.344	578175.2	1.778	438564.6	3.556	877129.3	0.889	219282.3	1.778	438564.6
Small Pelagics- squid	1.414	348779.7	1.2675	312643.8	2.535	625287.6	0.63375	156321.9	1.2675	312643.8
Small Pelagics- anadromous	0.889	219282.3	0.1	24666.18	0.2	49332.35	0.05	12333.09	0.1	24666.18
Medium Pelagics- (piscivores & other)	0.563	138870.6	1.0406	256676.2	1.0406	256676.2	1.0406	256676.2	0.5203	128338.1
Demersals- benthivores	2.511	619367.7	7.473	1843303	7.473	1843303	7.473	1843303	3.7365	921651.7
Demersals- omnivores	2.927	721979	2.988	737025.4	2.988	737025.4	2.988	737025.4	1.494	368512.7
Demersals- piscivores	1.97	485923.7	4.581	1129958	4.581	1129958	4.581	1129958	2.2905	564978.8

Table 7. Systemic (or cybernetic) network metrics under the different scenarios.

	Baseline	Bmsy	Double Pel	Half Pel	Half Dem
Sum of all consumption	7317.092	7312.478	7361.06	7296.269	7315.869
Sum of all exports	766.187	771.497	748.048	775.166	766.834
Sum of all respiratory flows	3460.682	3455.371	3478.825	3451.702	3460.035
Sum of all flows into detritus	4234.077	4239.554	4237.845	4243.863	4234.798
Total system throughput	15778	15779	15826	15767	15778
Sum of all production	6229	6229	6238	6221	6226
Mean trophic level of the catch	2.97	2.97	2.97	2.96	2.96
Gross efficiency (catch/net p.p.)	0.003434	0.003434	0.003434	0.003434	0.003434
Input total net primary production					
Calculated total net primary production	4227.27	4227.27	4227.27	4227.27	4227.27
Unaccounted primary production					
Total primary production/total respiration	1.222	1.223	1.215	1.225	1.222
Net system production	766.588	771.899	748.445	775.568	767.235
Total primary production/total biomass	27.33	27.241	26.041	27.679	27.446
Total biomass/total throughput	0.01	0.01	0.01	0.01	0.01
Total biomass (excluding detritus)	154.675	155.181	162.33	152.723	154.021
Total catches	14.518	14.518	14.518	14.518	14.518
Connectance Index	0.334	0.334	0.334	0.334	0.334
System Omnivory Index	0.282	0.284	0.283	0.278	0.281
Total market value	10.17	10.17	10.17	10.17	10.17
Total shadow value	0	0	0	0	0
Total value	10.17	10.17	10.17	10.17	10.17
Total fixed cost	3.36	3.36	3.36	3.36	3.36
Total variable cost	5.59	5.59	5.59	5.59	5.59
Total cost	8.95	8.95	8.95	8.95	8.95
Profit	1.22	1.22	1.22	1.22	1.22

Table 8. Summary of the composite fish group nodes under the different scenarios. Results are presented on an areal and absolute basis and represent the final, rebalanced model outputs.

	t km-2	Baseline	Bmsy	Double Pelagics	Halve Pelagics	Halve Demersals
Sum Pelagic Fish	mt	15.156	14.96	18.427	13.035	14.85
Sum Demersal Fish		7.971	8.485	11.173	8.19	7.814
Sum Fish		23.127	23.445	29.6	21.225	22.664
Sum Pelagic Fish		3738405	3690060	4545236	3215236	3662927
Sum Demersal Fish		1966140	2092925	2755951	2020159	1927415
Sum Fish		5704546	5782985	7301188	5235396	5590342

Figure Legends.

Figure 1. A. Change in absolute predicted biomass (metric tons) of small pelagic and demersal fish nodes under the B_{MSY} scenario with respect to the initial scenario inputs and the baseline, balanced model. B. Change as a percent difference of small pelagic and demersal fish nodes under the B_{MSY} scenario with respect to the initial scenario inputs and the baseline, balanced model.

Figure 2. A. Change in absolute predicted biomass (metric tons) of small pelagic and demersal fish nodes under the doubling small pelagics scenario with respect to the initial scenario inputs and the baseline, balanced model. B. Change as a percent difference of small pelagic and demersal fish nodes under the doubling small pelagics scenario with respect to the initial scenario inputs and the baseline, balanced model.

Figure 3. A. Change in absolute predicted biomass (metric tons) of small pelagic and demersal fish nodes under the halving small pelagics scenario with respect to the initial scenario inputs and the baseline, balanced model. B. Change as a percent difference of small pelagic and demersal fish nodes under the halving small pelagics scenario with respect to the initial scenario inputs and the baseline, balanced model.

Figure 4. A. Change in absolute predicted biomass (metric tons) of small pelagic and demersal fish nodes under the halving demersals scenario with respect to the initial scenario inputs and the baseline, balanced model. B. Change as a percent difference of small pelagic and demersal fish nodes under the halving demersals scenario with respect to the initial scenario inputs and the baseline, balanced model.

Figure 5. Flows to detritus for the eight main fish nodes under the different scenarios.